Vol. 48 No. 9

BULLETIN

OF THE

TORREY BOTANICAL CLUB

SEPTEMBER, 1921

The air chambers of Reboulia hemisphaerica

(WITH TWENTY-TWO TEXT FIGURES)

A. W. DUPLER

INTRODUCTION

The air chambers of the Marchantiales may be grouped under the three categories outlined by Leitgeb (12, 13, 14). These categories, named after characteristic genera, were defined by him essentially as follows: 1, the *Riccia* type, with simple air chambers, the chlorophyll being in the wall cells; 2, the *Marchantia* type, in which the simple chambers contain filaments of chlorophyllose cells; and 3, the *Reboulia* type, in which the primary chambers are more or less divided into secondary chambers by plates of cells arising from the sides, floor and even roof of the primary chambers. While the *Reboulia* type of chamber has been studied in other genera, *Reboulia* itself has received very little attention.

HISTORICAL

In the literature dealing with the air chambers of the Marchantiales two general problems have arisen, so far as the *Reboulia* type is concerned. The first of these has to do with the question whether the subdivisions of the primary chambers are due to ingrowths into the primary chamber or arise as a result of schizogenous splitting of the thallus tissue. The second and more fundamental problem has to do with the origin and early development

[The BULLETIN for August (48: 219–240) was issued October 21, 1921.]

of the air chambers. In this connection two points of view have been emphasized, viz., that of Leitgeb (12, 13, 14), who regarded them as formed by a dorsal upgrowth arising from superficial cells, and that of Barnes and Land (1), who pointed out the internal schizogenous origin of the air chambers. A summary of the earlier literature dealing with this problem, dating back to Hofmeister (11), is to be found in the paper by Barnes and Land; while the later literature has been reviewed by Evans (7). In the present paper reference is made to the recent literature only when it bears somewhat directly on *Reboulia* itself or its close allies.

Leitgeb's interpretation of the structure and partitioning of the air chambers of *Reboulia*, as noted above, has been generally accepted by such writers as Cavers (4, 5), Campbell (3), and Goebel (8). Cavers notes that near the apex there is but a single layer of chambers, each with a simple pore, but that the chambers become partitioned as they develop. Campbell holds for *Reboulia* and *Fimbriaria* (*F. californica* is especially described) that there is a more or less complete division of the primary chambers by the formation of diaphragms. Barnes and Land (1) state that in *Plagiochasma* it appears probable that the partitioning of the chambers occurs as described by Leitgeb but that "the formation of the aerating tissue is mainly due to splitting and growth." From her study of *Plagiochasma* (*Aytonia*) Miss Starr (16) claims that Leitgeb's partitioning plates are not outgrowths but arise by "stretching and tearing of tissues between neighboring chambers . . . the tearing being due to the differences in tension between the upper and lower parts of the thallus. This leaves projecting plates of cells, appearing as filaments in section, which Leitgeb and Campbell interpreted as new growth dividing the original chambers. Perhaps these plates add to their length by further growth." Evans (7) has made a very careful study of the air chambers in *Grimaldia fragrans*, and his results are of importance in a comparison with *Reboulia*. He finds that the primary chambers of the dorsal region "are subdivided by an irregular system of more or less vertical, united cell plates, enclosing narrow spaces, so that the boundaries of the chambers are difficult to distinguish." He finds that these plates may end freely below the epidermis or extend to the epidermis but that "it is doubtful . . . if the connec-

tion is anything more than a close contact." He adds further, "no instance has been observed where an outgrowth extends downward from the epidermis and ends freely in a chamber, and there is no adequate evidence that the epidermal cells themselves ever give rise to outgrowths." He finds the "more deeply situated" chambers simple and usually without any partitioning cell plates. The secondary partitions apparently arise as outgrowths from the floor, as one would interpret the statement, "as the writer conceives the process, the growth of the partitions is both horizontal and vertical, the growth in the latter direction being often equalled by the upward growth (accompanied by cell division) of the cells forming the floors of the chambers; these in turn remain more or less united with one another and with the cells of the partitions and in this way form the system of united cell-plates in the dorsal chambers." In a study of the chambers of the female receptacle surface outgrowths from the partitions themselves are found, but "in the vegetative thallus such outgrowths evidently play a very minor part in the development of the green tissue." Evans concludes further that the increase in size of the chambers is due largely to the growth of the bounding cells, differing in this respect from Miss Starr in her interpretation of the situation in *Plagiochasma*. Haupt (**9**) describes the air chambers of *Reboulia* but does not consider the problem of the origin and development of the internal partitions.

With regard to the problem of the origin of the air chambers Leitgeb based his theory of the superficial origin by upgrowth on a study of the Ricciaceae (**12**) but later (**13, 14**) applied it to the Marchantiaceae as well. His theory remained unquestioned for some time, even in view of his own admission that at least a part of the air chambers seemed to arise schizogenously in *Reboulia* and *Plagiochasma*. Barnes and Land (**1**) controverted Leitgeb's idea, replacing it by one which accounts for the origin of the air chambers in the Marchantiales as "arising invariably by the splitting of internal cell walls, usually at the junction of the outermost and first internal layer of cells." Of the forms with the *Reboulia* type of chamber they studied *Fimbriaria* (probably *F. echinella* Gottsche) and *Plagiochasma* sp., finding in the former that "the primary splitting usually begins between the cells

arising from successive segments. . . . Later, and often deep in the tissue, secondary splitting gives rise to intercellular spaces which may reach the surface or may break into a primary space. In *Plagiochasma* the situation is similar only the secondary splitting occurs more quickly and becomes quite extensive. The passages are not wide and shallow, but always deep and narrow open almost or quite uninterruptedly until the pore margin is well begun."

The problem thus opened up anew was attacked by different writers, dealing largely with the Ricciaceae and *Targionia*. Miss Hirsch (10) and Miss Black (2) both support the Leitgeb view for *Riccia Frostii*. Campbell (3) regards their work, as well as that of Miss O'Keefe (15), as showing that Leitgeb's account of the formation of air spaces in *Riccia glauca* and other allied species is entirely correct. Both Deutsch (6) and Miss O'Keefe (15), in their studies of *Targionia hypophylla*, agree that the chambers arise by splitting, but that the splitting begins superficially and proceeds inward, instead of arising internally and proceeding outward. Miss Starr's study of *Plagiochasma* (16) leads her to conclude that there is no doubt as to the internal schizogenous origin of the air chambers of both thallus and receptacle. The development of the barrel-shaped air-pore on the receptacle is described in detail. Evans (7) reviews the recent work on the problem pointing out that in all cases, even including the work of Miss Hirsch and Miss Black, the origin of the air chambers is probably due to splitting of the cell walls, although it may begin superficially in some cases. From his study of *Grimaldia fragrans* he concludes that "the chambers all owe their origin to a splitting of cell walls in closely united tissue. In the case of the dorsal chambers the split sometimes begins below the surface and extends outward, sometimes at the surface and extends inward." Further, "that there still seems to be no conclusive evidence that Leitgeb's explanation ever applies." Haupt (9) in his recent study of *Reboulia hemisphaerica* states that "the air chambers of *Reboulia* arise immediately behind the apical cell of the thallus by intercellular splittings which start at the surface of the thallus and progress inward, reaching the line of differentiation between the dorsal and ventral regions. Secondary splittings occur deep within the dorsal region and do not reach the surface." No

account of the development of the chambers of the receptacle is given by either Evans or Haupt for the two forms which they studied.

AIR CHAMBERS OF THE THALLUS

Mature features.—In such forms as *Marchantia* and *Conocephalum* surface markings indicate the internal chambers, but *Reboulia* and its allies have no such external markings, the upper

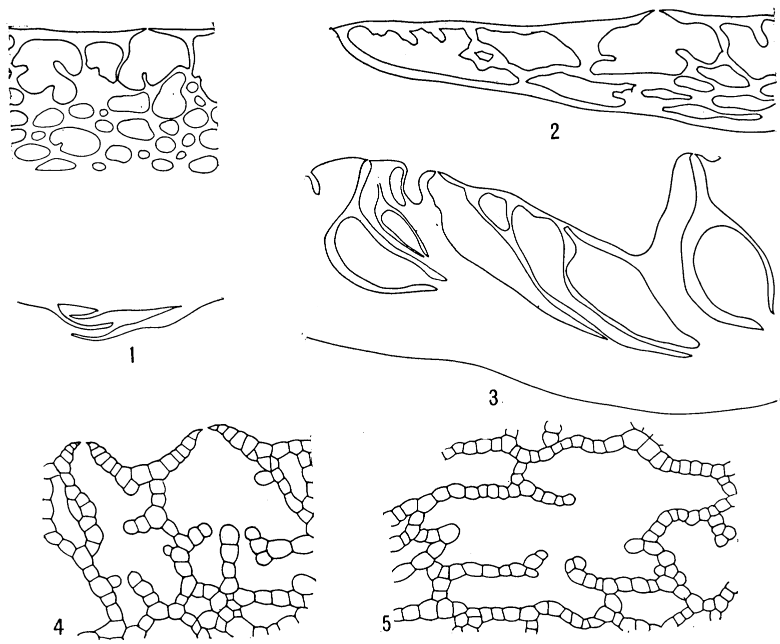


FIG. 1. Transverse section of a mature thallus, in the midrib region, x 40. FIG. 2. Transverse section of a mature thallus, along the margin, x 40. FIG. 3. Longitudinal section of a mature thallus between two antheridial receptacles, showing the single series of chambers, overlapping shingle-like and extending from the surface to the compact tissue, x 40. FIG. 4. Transverse section through the dorsal portion of the air-chamber tissue, x 82. FIG. 5. Section through a small air chamber cut parallel with the surface, x 82.

surface being uniform in color and smooth except for the very slight conical projections with air-pores in the center. Whole mounts of the thallus, stained *in toto*, show that the very elongated air chambers extend lengthwise along the midrib and from this

radiate pinnately toward the margin. The secondary partitions are for the most part parallel with or slightly oblique to the primary walls, and give a very areolated structure to the thallus, only the number and distribution of the air pores giving any indication as to the primary chambers. A cross section of the thallus in the midrib region shows several layers of superimposed chambers in this region (FIG. 1), the chambers being gradually reduced to a single layer along the margin (FIG. 2). The compact ventral tissue also gradually becomes narrower until at the margin of the thallus it is usually only a single layer of cells in thickness. Longitudinal sections (FIG. 3) show that this appearance of superimposed chambers is due largely, if indeed not altogether, to an extensive shingle-like overlapping of the primary chambers, greatly complicated by the formation of partial secondary chambers by partitions which form in the chambers. These primary chambers extend from the surface to the compact ventral tissue. Of course, "deeper" chambers appear in sections cut in almost any direction, but a careful study of these chambers through a complete series of sections shows them to be largely the more deeply situated portions of the primary chambers. Where the tissue is more compact, as in *Plagiochasma* and *Grimaldia fragrans*, the deep secondary chambers may be more probable. An examination of a few preparations of *Neesiella rupestris* indicates that the interpretation here applied to *Reboulia* also applies to that form, which has a more simply organized tissue than *Reboulia*. Cross sections give an appearance similar to that described for *Grimaldia* by Evans (7), the dorsal chambers being partially subdivided by plate-like outgrowths arising from the sides and floor of the chambers. Sections parallel to the surface are helpful in the interpretation of the structure (FIG. 5). It is very doubtful whether any plates arise from the roof of the chamber and project downwards into the chambers, the appearance of this in sections being due to the oblique inclination of the plates. Many of these secondary plates come in contact with the roof of the chambers. The primary partitions, the secondary plates and the roof of the chamber are all but a single layer of cells in thickness. Occasionally the cone formed by the air-pore projects inward into the chamber, this condition being associated with the portion of the thallus immediately posterior to the male receptacle.

Origin and development.—The young chambers evidently arise schizogenously, the splitting beginning as close to the apical cell as between the third and fourth segments (FIGS. 6, 8). The splitting probably begins internally (FIG. 7), although a superficial splitting is also initiated very soon, and the process apparently proceeds simultaneously from both these points, the two splits meeting about midway (FIGS. 6, 8). The turgor conditions which effect splitting can reasonably bring about external as well as internal separation. As the thallus thickens back of the apex the splitting may continue to deeper levels, although the increased

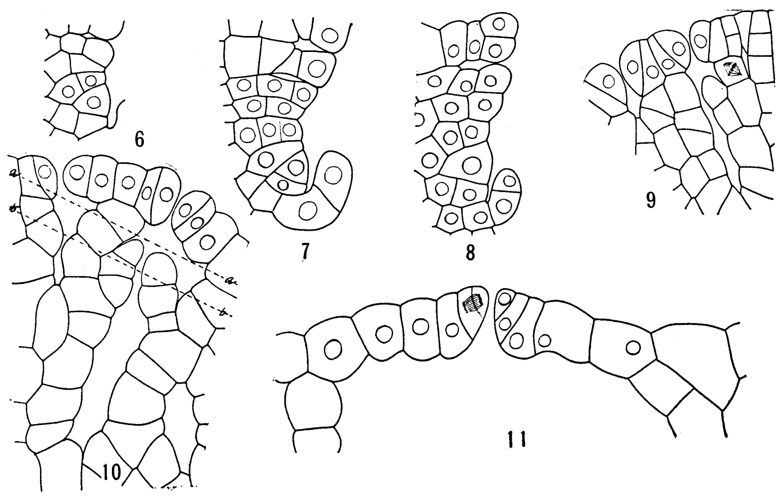


FIG. 6. Longitudinal section through a growing point, showing the apical cell and the beginning of an air chamber, with both internal and superficial splitting, x 433. FIG. 7. Similar section, showing air chamber with internal origin, x 433. FIG. 8. Similar section with slightly older air chamber, x 433. FIG. 9. Longitudinal section of young air chambers, showing beginning of secondary partitioning and intercalary division in the primary partition, x 433. FIG. 10. Air chamber a little older than that of FIG. 9, x 433. FIG. 11. Epidermis of a nearly mature chamber, x 433.

depth of the chambers is due in large part to intercalary growth of the partitions themselves (FIG. 14). The earliest chambers are horizontal but with the growth of the thallus become obliquely inclined. Early in the development of the chambers the secondary plates have their origin as lateral outgrowths from the primary partitions (FIGS. 9, 10). These are so situated in the narrow

chambers as to give the appearance in section (FIG. 10) of narrow passage ways between "dorsal" and "more deeply situated" chambers, though in fact but lateral outgrowths of the primary chambers. They arise at different levels and contribute to the complex network of the mature thallus. I find no indication of secondary splitting in the compact tissue. Chambers appearing as such are easily found, but when traced always show connections with the surface chambers. A section of FIG. 10 along the line *aa* would show a few large chambers. One at the level *bb* would show smaller but more numerous spaces between the cells, an appearance similar to that shown by Evans (7, *f. 11, 12*) for *Grimaldia*. His *f. 13* of a longitudinal section of the same stage is essentially like that of FIG. 10 and would lend itself to the same interpretation as is here made for *Reboulia*.

The single superficial cell of the partition (FIG. 7) soon divides into segments, and a circle of triangular cells around the young pore is thus formed. These divide by oblique tangential walls (FIG. 9), forming the first circle of the actual air-pore cells. Continued divisions (FIGS. 10, 11) build up the series of concentric circles surrounding the simple pore.

THE FEMALE RECEPTACLE

At first the young female receptacle consists of a very compact tissue, air chambers not appearing until after the archegonia have started their development (FIGS. 12, 13). The first air chambers are formed at the crest of the young receptacle (FIG. 13) but with the growth of the latter appear nearer the archegonia (FIGS. 14, 15). The young chambers arise by internal splitting, but superficial splitting also begins very soon and the two proceed simultaneously just as in the thallus (FIGS. 13, 14). The internal split extends to a depth of but a few layers of cells (FIG. 16), increase in depth and diameter being due to intercalary growth of the partitions, which remain but one cell layer thick. The chambers become obliquely pyramidal (FIGS. 19, 21), with the apex pointing toward the center of the receptacle, and overlap one another at maturity, as in the case of the thallus only to a less extent. I found no indication of secondary deep splitting on the young receptacle and see no necessity for interpreting the mature struc-

ture as due to the occurrence of such splitting. Projecting into the primary chambers are cell plates, beginning while the chambers are yet quite small (FIG. 21) and becoming quite pronounced by the time of maturity.

A surface view of the young receptacles (FIG. 17) shows that young air chambers arise at most of the intersection points of the cells dorsal to the archegonia, the young pores being bounded originally by four or five cells which in vertical section appear papillate (FIG. 13). The primary bounding cells then divide by walls extending from pore to pore, forming a circle of wedge-shaped

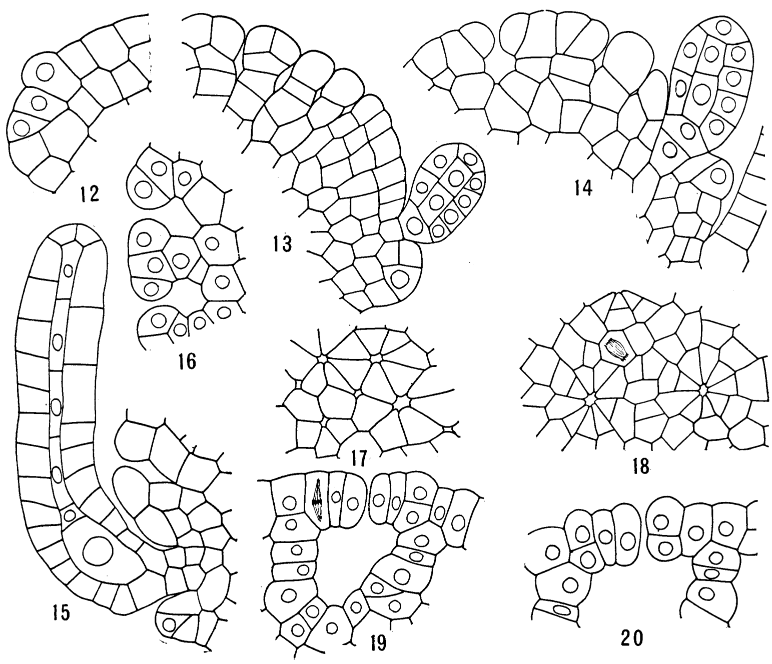
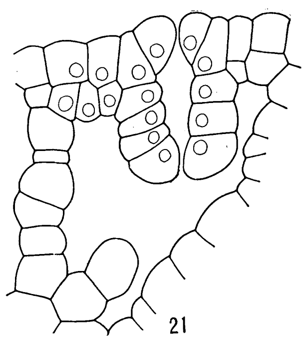


FIG. 12. Section through a young female receptacle, showing the apical cell and archegonium initial. At this stage there is no indication of air chamber formation, x 433. FIG. 13. Young receptacle showing oldest air chambers at the crest. The tissue near the archegonium is yet compact, x 433. FIG. 14. Air chambers more advanced than in FIG. 13, x 433. FIG. 15. Young air chamber immediately dorsal to the archegonium, x 433. FIG. 16. Air chambers nearer the crest of same receptacle as FIG. 15, x 433. FIG. 17. Surface view of young receptacle, showing beginning of air chambers, same stage as FIG. 13, x 433. FIG. 18. Surface view of older receptacle, x 433. FIG. 19. Vertical section of a young chamber, x 433. FIG. 20. Beginning of the barrel-pore of the female receptacle, x 433.

cells around the pore (FIG. 17). Divisions tangential to the pore begin the formation of the roof of the chamber, forming a circle of small wedge-shaped cells (FIG. 18). As development proceeds the chambers become wider (FIGS. 19–21), the growth of the roof keeping pace. At first the roof consists of but a single layer of cells, but very early in development periclinal divisions occur, usually beginning at the margins of the chamber (FIG. 19) and proceeding until the roof becomes, as a rule, two cells in thickness (FIG. 21). Very short outgrowths may project from the roof into the chamber.



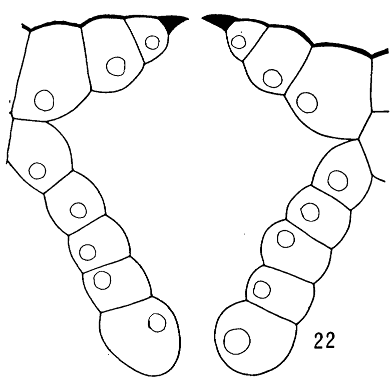


FIG. 21. Vertical section of a young chamber, showing the nearly complete barrel-pore and a secondary plate projecting into the chamber, x 433. FIG. 22. Mature pore on female receptacle, x 433.

In sharp contrast to the simple pores of the thallus are the large barrel-shaped pores of the female receptacle. Usually the young pore is open from the start, differing in this respect from the young pores of *Plagiochasma* as shown by Miss Starr (**16**). The "barrel" is formed by periclinal divisions of the circle of cells forming the margin of the young pore. The first division results in an inner and an outer tier of cells (FIG. 20). The inner tier by a series of divisions forms the portion projecting into the chamber; the outer tier by a series of similar but later divisions gives rise to the outer portion of the pore (FIG. 21). The inner projection of the pore consists of five or six tiers of cells, the outer of three or four, the circle next the pore becoming cutinized at maturity (FIG. 22).

THE MALE RECEPTACLE

The tissue of the male receptacle is compact, aside from the antheridial chambers and very few air chambers appear on the disc. These are situated along the margins and are relatively simple in structure, containing only simple pores. In this respect the writer's observations agree with those of Haupt (**9**) but differ from those of Cavers (**4**, **5**), who described and figured small barrel-shaped pores in the male receptacle of *Reboulia hemisphaerica*.

SUMMARY

The very elongated air chambers of the thallus extend lengthwise along the midrib region and from this radiate pinnately toward the margins of the thallus.

The air chamber tissue consists essentially of a single series of oblique chambers extending from the surface to the compact tissue, overlapping one another shingle-like and thus giving the appearance in section of several series of superimposed chambers.

The primary chambers are extensively subdivided into partial secondary chambers by plates of cells arising as lateral outgrowths of the primary walls.

The air chambers of both thallus and receptacles originate by splitting of cell membranes, the splits arising both internally and superficially, and generally proceeding from both points of origin simultaneously.

The later development of the chambers and the secondary partitioning is due largely to growth of the tissues, further splitting apparently playing but a small rôle in the process.

JUNIATA COLLEGE,
HUNTINGDON, PENNSYLVANIA

LITERATURE CITED

1. **Barnes, C. R., & Land, W. J. G.** Bryological papers. I. The origin of air chambers. Bot. Gaz. **44**: 197–213. *f. 1–22.* 1907.
2. **Black, C. A.** The morphology of *Riccia Frostii*, Aust. Ann. Bot. **27**: 511–532. *pl. 37, 38.* 1913.
3. **Campbell, D. H.** Mosses and Ferns. 3d ed. New York. 1918.
4. **Cavers, F.** Contributions to the biology of the Hepaticae. Part I. *Targionia*, *Reboulia*, *Preissia*, *Monoclea*. Leeds and London. 1904.

5. —— Notes on Yorkshire Bryophytes. III. *Reboulia hemisphaerica* (L.) Raddi. Naturalist 1904: [1–15]. *pl. 8* + *f. 2–6.* 1904.
6. **Deutsch, H.** A study of *Targionia hypophylla.* Bot. Gaz. **53**: 492–503. *f. 1–13.* 1912.
7. **Evans, A. W.** The air chambers of *Grimaldia fragrans.* Bull. Torrey Club **45**: 235–251. *f. 1–14.* 1918.
8. **Goebel, K.** Organographie der Pflanzen. II. Spezielle Organographie. 2d ed. **1**. Bryophyten. Jena. 1915.
9. **Haupt, A. W.** The gametophyte and sex organs of *Reboulia hemisphaerica.* Bot. Gaz. **71**: 61–74. *f. 1–21.* 1921.
10. **Hirsh, P.** The development of the air chambers in the Ricciaceae. Bull. Torrey Club. **37**: 73–77. *f. 1–6.* 1910.
11. **Hofmeister, W.** Higher Cryptogamia. Eng. ed. London. 1862.
12. **Leitgeb, H.** Untersuchungen über die Lebermoose. 4. Die Ricceen. Graz. 1879.
13. —— Die Athemöffnungen der Marchantiaceen. Sitzb. Kais. Akad. Wiss. Wien **81**: 40–54. *pl. 1.* 1880.
14. —— Untersuchungen über die Lebermoose. 6. Die Marchantieen und allgemeine Bemerkungen über Lebermoose. Graz. 1881.
15. **O'Keefe, L.** Structure and development of *Targionia hypophylla.* New Phytol. **14**: 105–116. *f. 1, 2.* 1915.
16. **Starr, A. M.** A Mexican *Aytonia.* Bot. Gaz. **61**: 48–58. *pl. 1–4* + *f. 30–33.* 1916.